ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 35: 165–178 (2022)
DOI 10.3897/herpetozoa.35.e89981

A new species of the genus *Leptobrachella* (Anura, Megophryidae) from northwestern Guangdong Province, China

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https://zoobank.org/A2298822-46FC-4077-8F66-7A0E7840C174

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Academic editor: Günter Gollmann ♦ **Received** 6 July 2022 ♦ **Accepted** 19 September 2022 ♦ **Published** 28 September 2022

Abstract

The genus *Leptobrachella* is a species-rich genus of megophrid frog. Rapid discovery of many new species within this genus emphasizes the importance of regional research. In this study, we describe a new species of *Leptobrachella*, *Leptobrachella verrucosa* **sp. nov.**, from northwestern Guangdong Province, China, based on a combination of molecular and morphological data. A key including congeners from the same province, namely *L. laui*, *L. liui*, *L. mangshanensis*, *L. shimentaina*, and *L. yunkaiensis*, is provided.

Key Words

Leptobrachella verrucosa sp. nov., molecular phylogeny, morphology, taxonomy

Introduction

Frogs of the genus *Leptobrachella* Smith, 1925, are forest dwellers that are widely distributed in China, Myanmar, northeastern India, the Indochina region, Borneo and Natuna Island (AmphibiaWeb 2022; Frost 2022). *Leptobrachella* represents one of the most species-rich groups of frogs with 93 recognized species. However, the morphological conservativeness of this group makes it hard to study their taxonomy, hindering our understanding of the true diversity of this group (Wang et al. 2019). Combining detailed morphological examination and molecular phylogeny, Wang et al. (2022) clarified the taxonomic status of the *Leptobrachella* populations in Guangdong Province, China, and confirmed the occurrence of *L. laui* (Sung, Yang & Wang, 2014), *L. liui* (Fei & Ye, 1990), *L. mangshanensis* (Hou, Zhang, Hu, Li, Shi, Chen, Mo & Wang, 2018), *L. shimentaina* Wang, Lyu & Wang, 2022 and *L. yunkaiensis* Wang, Li, Lyu & Wang, 2018 (Fig. 1), and simultaneously ruled out the distribution of *L. pelodytoides* (Boulenger, 1893) in the province. This reflects the high diversity of *Leptobrachella* in Guangdong Province, and also emphasizes the need to produce a provincial checklist and study the distribution pattern of these frogs.

* These authors contributed equally to this work.

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During recent field surveys in mountainous areas of northwestern Guangdong which border with Hunan Province and Guangxi Zhuang Autonomous Region (Fig. 1), we collected five adult male specimens of *Leptobrachella*. Preliminary morphological examination indicated that they can be distinguished from recognized congeners by a series of discrete features. Subsequent molecular analysis further revealed that these specimens represent a separate evolutionary lineage. Considering both the morphological differences and their genetic allocation and divergences, these specimens are described herein as a new species. A key for congeners that occur in Guangdong Province is also provided.

Materials and methods

Phylogenetic analyses

In total, 108 samples of 80 *Leptobrachella* species plus 2 outgroup samples were used in this study, encompassing five newly sequenced individuals and others downloaded from GenBank. Detailed information for all samples is given in Suppl. material 1: Table S1. All newly collected specimens were euthanized with MS 222 and fixed in 10% buffered formalin and later transferred to 70% ethanol for preservation, and deposited at the Guangdong Polytechnic of Environmental Protection Engineering (**GEP**), Foshan City, Guangdong, China; muscle tissue samples were preserved in 95% ethanol for molecular studies.

The 16S ribosomal RNA mitochondrial gene (16S rRNA) fragment of 528 base pairs was sequenced for new samples; DNA extraction, PCR, and sequencing follow Wang et al. (2020). Sequences were aligned with Clustal X 2.0 (Thompson et al. 1997) with default parameters. We ran Jmodeltest v2.1.2 (Darriba et al. 2012; with Akaike and Bayesian information criteria) on our alignment and obtained the best-fitting nucleotide substitution model of GTR + I + G (General Time Reversible model, with variable sites modelled according to the Gamma distribution, and a portion of the sites invariant). Phylogenetic analysis was conducted using Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012) and maximum likelihood (ML) in maximum likelihood (ML) in Randomized Axelerated Maximum Likelihood (RAxML, Stamatakis 2006) with RAxML GUI 1.3 (Silvestro and Michalak 2012). For the ML analysis, an optimal tree was obtained and branch supports were evaluated with 1000 rapid bootstrapping replicates. For the BI analysis, two independent runs with four Markov Chain Monte Carlo simulations were performed for ten million iterations and sampled every 1000 iterations. The first 25% of the samples were discarded as burn-in, leaving 7500 samples in the final summary. Convergence of the Markov Chain Monte Carlo simulations was assessed by PSRF < 0.01 and ESS (effective sample size) value > 200 using Tracer 1.4 (http://tree.bio.ed.ac.uk/software/tracer/). Nodes having ML bootstrap values (BS) ≥ 70 and BI posterior probabilities (BPP) ≥ 0.90 were considered well supported. Genetic distances among all *Leptobrachella* samples were calculated in MEGA 6 using the uncorrected *p*-distance model.

Morphological examination

Following Fei et al. (2009) and Rowley et al. (2013), measurements were taken with digital calipers from preserved specimens (Neiko 01407A Stainless Steel 6-Inch Digital Calipers) to the nearest 0.1 mm. Measurements include: snout-vent length (**SVL**) from the tip of the snout to posterior margin of the vent; head length (**HDL**) from the tip of the snout to the articulation of the jaw; head width (**HDW**) at the commissure of the jaws; snout length (**SNT**) from the tip of the snout to the anterior corner of the eye; eye diameter (**EYE**) from the anterior corner of the eye to posterior corner of the eye; internasal distance (**IND**); interorbital distance (**IOD**); horizontal diameter of tympanum (**TMP**); tympanum-eye distance (**TEY**) from the anterior edge of tympanum to posterior corner of the eye; tibial length (**TIB**) from the outer surface of the flexed knee to the heel; manus length (**ML**) from the tip of the third finger to the proximal edge of inner palmar tubercle; pes length (**PE**) from the tip of the fourth toe to the proximal edge of the inner metatarsal tubercle; length of lower arm and hand (**LAHL**) from the tip of the third finger to elbow; and hindlimb length (**HLL**) from the tip of the fourth toe to vent.

Sex was determined by direct observation of calling in life. Comparative morphological data for other congeneric species of *Leptobrachella* were obtained from museum specimens (Appendix 1) and from the literature (Table 1).

Results

The ML and Bayesian approach results identical topologies, and all *Leptobrachella* samples form a monophyletic clade strongly-supported in both phylogenetic trees (Fig. 2). The *Leptobrachella* samples (ID 1–5, Suppl. material 1: Table S1) from Lianshan Bijiashan Nature Reserve form a monophyletic clade which is strongly supported (BS = 100; BPP = 1.00). This clade represents an independent lineage with strong divergence and it is grouped with the clade composed of *L. liui* and *L. mangshanensis*. However, the relationship of these three lineages is not well resolved.

Although we did not use genetic distances to diagnose the new species (which we define on the basis of discrete character differences), we note that the *Leptobrachella* lineage from Lianshan Bijiashan Nature Reserve differs from its closely-related congeners by 2.4% (with *L. liui*) and 2.6% (with *L. mangshanensis*) in the mean *p*-distance of 16S RNA ribosomal mitochondrial gene (Suppl. material 2: Table S2), which approximates the level of genetic divergence observed in uncontroversial species of *Leptobrachella*:

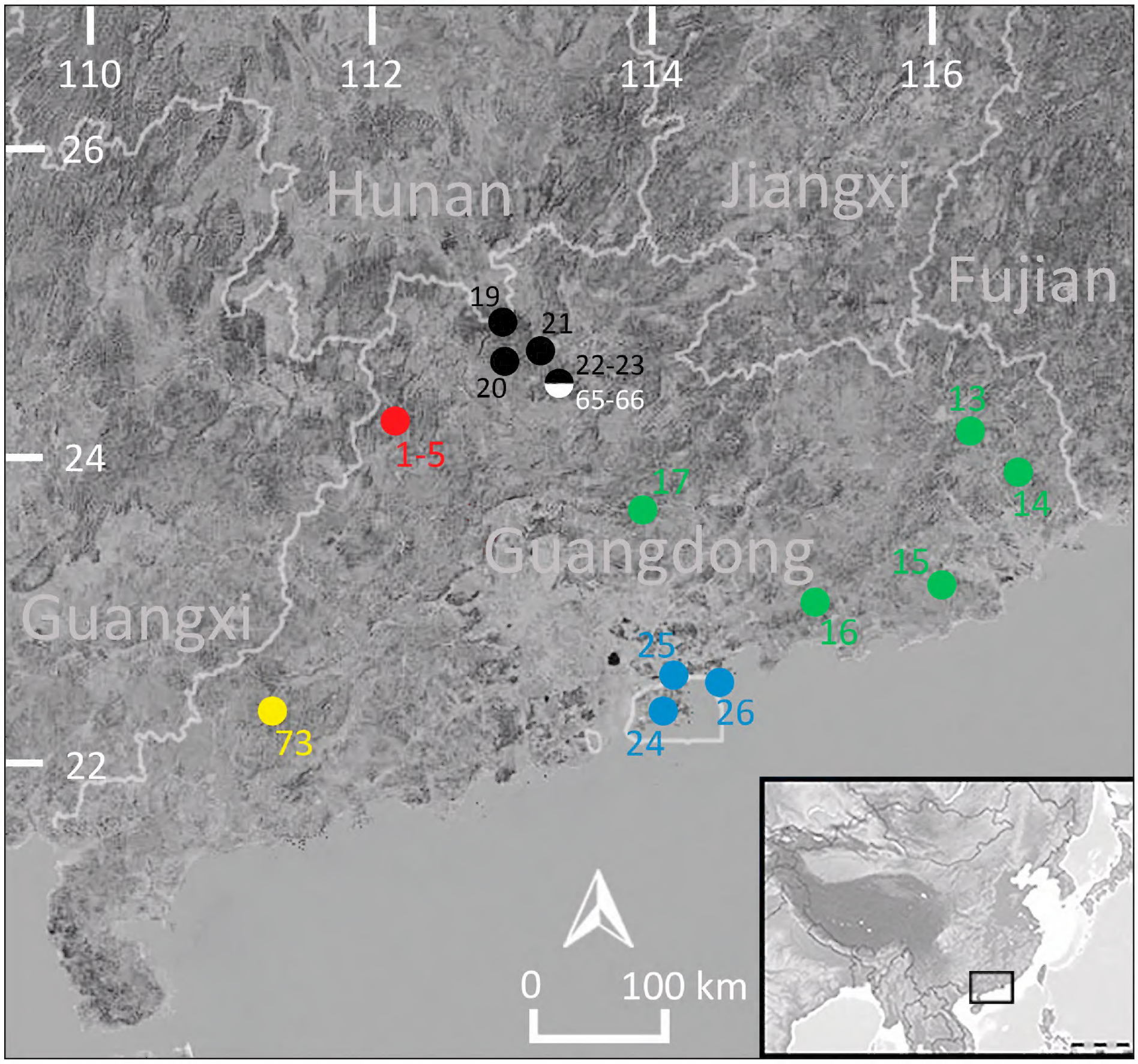

Figure 1. Localities of *Leptobrachella* species occurring in Guangdong Province and Hong Kong, China: *Leptobrachella verrucosa* sp. nov. (samples ID 1–5, Lianshan Bijiashan Nature Reserve, Lianshan county); *L. mangshanensis* (sample ID 19, Nanling Nature Reserve, Ruyuan county; sample ID 20, Mt. Tianjing, Ruyuan county; sample ID 21, Mt. Dadong, Lianxian county; samples ID 22–23, Shimentai Nature Reserve, Yingde city); *L. liui* (sample ID 13, Mt. Tongguzhang, Fengshun county; sample ID 14, Mt. Fenghuang, Chaozhou city; sample ID 15, Mt. Motianshi, Puning city; sample ID 16, Baipenzhu, Huidong county; sample ID 17, Mt. Nankun, Longmen county); *L. laui* (sample ID 24, Tai Mo Shan, Hong Kong; sample ID 25, Mt. Wutong, Shenzhen city; sample ID 26, Mt. Paiya, Shenzhen city); *L. shimentaina* (sample ID 65, Shimentai Nature Reserve, Yingde city; sample ID 66, Luokeng Nature Reserve, Qujiang district); and *L. yunkaiensis* (sample ID 73, Mt. Yunkai, Xinyi city). Numbers correspond to the ID numbers in Suppl. material 1: Table S1.

1.9% between *L. liui* and *L. mangshanensis*, 2.3% between *L. liui* and *L. shimentaina*, 2.2% between *L. shimentaina* and *L. mangshanensis*, 1.7% between *L. eos* and *L. dorsospina*, 1.7% between *L. bourreti* and *L. eos*, 1.7% between *L. bourreti* and *L. graminicola*, 1.3% between *L. jinshaensis* and *L. niveimontis*, 2.3% between *L. bijie* and *L. jinshaensis*, 1.7% between *L. bourreti* and *L. wulingensis*, 2.0% between *L. dorsospina* and *L. wulingensis*, 1.3% between *L.chishuiensis* and *L.bijie*, 1.3% between *L.purpurus* and *L.alpina*, 1.7% between *L.purpurus* and *L.juliangdringi*, 1.7% between *L.purpurus* and *L. niveimontis*, 1.3% between *L.pelodytoides* and *L. ventripunctata*, and 2.0% between *L. eos* and *L. wulingensis*.

Our detailed morphological examination has also revealed discrete, diagnostic (non-overlapping ranges in traditional characters) differences among the specimens from this independent lineage and all other congeners. Therefore, both phylogenetic result and morphological comparison support the hypothesis that the lineage from Lianshan Bijiashan Nature Reserve represent an undescribed new species, and herein we describe this new species.

Table 1. Data source of the currently known species of the genus *Leptobrachella*.

ID	*Leptobrachella* species	Literature obtained
1	*L. aerea* (Rowley, Stuart, Richards, Phimmachak & Sivongxay, 2010c)	Rowley et al. 2010c
2	*L. aspera* Wang, Lyu, Qi & Wang, 2020	Wang et al. 2020
3	*L. alpina* (Fei, Ye & Li, 1990)	Fei et al. 1990; Fei et al. 2009, 2016
4	*L. applebyi* (Rowley & Cao, 2009)	Rowley and Cao 2009
5	*L. arayai* (Matsui, 1997)	Matsui 1997
6	*L. ardens* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
7	*L. baluensis* Smith, 1931	Dring 1983; Eto et al. 2016
8	*L. bashaensis* Lyu, Dai, Wei, He, Yuan, Shi, Zhou, Ran, Kuang, Guo, Wei & Yuan, 2020	Lyu et al. 2020a
9	*L. bijie* Wang, Li, Li, Chen & Wang, 2019	Wang et al. 2019, 2021
10	*L. bidoupensis* (Rowley, Le, Tran & Hoang, 2011)	Rowley et al. 2011
11	*L. bondangensis* Eto, Matsui, Hamidy, Munir & Iskandar, 2018	Eto et al. 2018
12	*L. botsfordi* (Rowley, Dau & Nguyen, 2013)	Rowley et al. 2013
13	*L. bourreti* (Dubois, 1983)	Ohler et al. 2011
14	*L. brevicrus* Dring, 1983	Dring 1983; Eto et al. 2015
15	*L. crocea* (Rowley, Hoang, Le, Dau & Cao, 2010)	Rowley et al. 2010a
16	*L. chishuiensis* Li, Liu, Wei & Wang, 2020	Li et al. 2020
17	*L. damingshanensis* Chen, Yu, Cheng, Meng, Wei, Zhou & Lu, 2021	Chen et al. 2021b
18	*L. dorsospina* Wang, Lyu, Qi & Wang, 2020	Wang et al. 2020
19	*L. dringi* (Dubois, 1987)	Inger et al. 1995; Matsui and Dehling 2012
20	*L. eos* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler & Dubois, 2011)	Ohler et al. 2011
21	*L. feii* Chen, Yuan & Che, 2020	Chen et al. 2020
22	*L. firthi* (Rowley, Hoang, Dau, Le & Cao, 2012)	Rowley et al. 2012
23	*L. fritinniens* (Dehling & Matsui, 2013)	Dehling and Matsui 2013
24	*L. fuliginosa* (Matsui, 2006)	Matsui 2006
25	*L. flaviglandulosa* Chen, Wang & Che, 2020	Chen et al. 2020
26	*L. fusca* Eto, Matsui, Hamidy, Munir & Iskandar, 2018	Eto et al. 2018
27	*L. gracilis* (Günther, 1872)	Günther 1872; Dehling 2012b
28	*L. hamidi* (Matsui, 1997)	Matsui 1997
29	*L. graminicola* Nguyen, Tapley, Nguyen, Luong & Rowley, 2021	Nguyen et al. 2021
30	*L. heteropus* (Boulenger, 1900)	Boulenger 1900
31	*L. isos* (Rowley, Stuart, Neang, Hoang, Dau, Nguyen & Emmett, 2015)	Rowley et al. 2015a
32	*L. itiokai* Eto, Matsui & Nishikawa, 2016	Eto et al. 2016
33	*L. juliandringi* Eto, Matsui & Nishikawa, 2015	Eto et al. 2015
34	*L. jinshaensis* Cheng, Shi, Li, Liu, Li & Wang, 2021	Cheng et al. 2021
35	*L. kajangensis* (Grismer, Grismer & Youmans, 2004)	Grismer et al. 2004
36	*L. kalonensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
37	*L. kecil* (Matsui, Belabut, Ahmad & Yong, 2009)	Matsui et al. 2009
38	*L. khasiorum* (Das, Tron, Rangad & Hooroo, 2010)	Das et al. 2010
39	*L. lateralis* (Anderson, 1871)	Anderson 1871; Humtsoe et al. 2008
40	*L. laui* (Sung, Yang & Wang, 2014)	Sung et al. 2014
41	*L. liui* (Fei & Ye, 1990)	Fei et al. 1990; Fei et al. 2009; Sung et al. 2014; Wang et al. 2022
42	*L. macrops* (Duong, Do, Ngo, Nguyen & Poyarkov, 2018)	Duong et al. 2018
43	*L. maculosa* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
44	*L. mangshanensis* (Hou, Zhang, Hu, Li, Shi, Chen, Mo & Wang, 2018)	Hou et al. 2018; Wang et al. 2022
45	*L. maoershanensis* (Yuan, Sun, Chen, Rowley & Che, 2017)	Yuan et al. 2017
46	*L. marmorata* (Matsui, Zainudin & Nishikawa, 2014b)	Matsui et al. 2014b
47	*L. maura* (Inger, Lakim, Biun & Yambun, 1997)	Inger et al. 1997
48	*L. melanoleuca* (Matsui, 2006)	Matsui 2006
49	*L. melica* (Rowley, Stuart, Neang & Emmett, 2010)	Rowley et al. 2010b
50	*L. minima* (Taylor, 1962)	Taylor 1962; Ohler et al. 2011
51	*L. mjobergi* Smith, 1925	Eto et al. 2015
52	*L. murphyi* Chen, Suwannapoom, Wu, Poyarkov, Xu, Pawangkhanant & Che, 2021	Chen et al. 2021a
53	*L. nahangensis* (Lathrop, Murphy, Orlov & Ho, 1998)	Lathrop et al. 1998
54	*L. natunae* (Günther, 1895)	Günther 1895
55	*L. namdongensis* Hoang, Nguyen, Luu, Nguyen & Jiang, 2019	Hoang et al. 2019
56	*L. neangi* Stuart & Rowley, 2020	Stuart and Rowley 2020
57	*L. niveimontis* Chen, Poyarkov, Yuan & Che, 2020	Chen et al. 2020
58	*L. nokrekensis* (Mathew & Sen, 2010)	Mathew and Sen 2010
59	*L. nyx* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler & Dubois, 2011)	Ohler et al. 2011
60	*L. oshanensis* (Liu, 1950)	Liu, 1950; Shi et al. 2021
61	*L. pallida* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016

ID	*Leptobrachella* species	Literature obtained
62	*L. palmata* Inger & Stuebing, 1992	Inger and Stuebing 1992
63	*L. parva* Dring, 1983	Dring 1983
64	*L. pelodytoides* (Boulenger, 1893)	Boulenger 1893; Ohler et al. 2011
65	*L. petrops* (Rowley, Dau, Hoang, Le, Cutajar & Nguyen, 2017)	Rowley et al. 2017a
66	*L. picta* (Malkmus, 1992)	Malkmus 1992
67	*L. platycephala* (Dehling, 2012)	Dehling 2012a
68	*L. pluvialis* (Ohler, Marquis, Swan & Grosjean, 2000)	Ohler et al. 2000, 2011
69	*L. puhoatensis* (Rowley, Dau & Cao, 2017)	Rowley et al. 2017b
70	*L. purpurus* (Yang, Zeng & Wang, 2018)	Yang et al. 2018
71	*L. purpuraventra* Wang, Li, Li, Chen & Wang, 2019	Wang et al. 2019
72	*L. pyrrhops* (Poyarkov, Rowley, Gogoleva, Vassilieva, Galoyan & Orlov, 2015)	Poyarkov et al. 2015
73	*L. rowleyae* (Nguyen, Poyarkov, Le, Vo, Ninh, Duong, Murphy & Sang, 2018)	Nguyen et al. 2018
74	*L. sabahmontana* (Matsui, Nishikawa & Yambun, 2014)	Matsui et al. 2014a
75	*L. serasanae* Dring, 1983	Dring 1983
76	*L. shangsiensis* Chen, Liao, Zhou & Mo, 2019	Chen et al. 2019
77	*L. shimentaina* Wang, Lyu & Wang, 2022	Wang et al. 2022
78	*L. sola* (Matsui, 2006)	Matsui 2006
79	*L. suiyangensis* Luo, Xiao, Gao & Zhou, 2020	Luo et al. 2020
80	*L. sungi* (Lathrop, Murphy, Orlov & Ho, 1998)	Lathrop et al. 1998
81	*L. shiwandashanensis* Chen, Peng, Pan, Liao, Liu & Huang, 2021	Chen et al. 2021c
82	*L. tadungensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
83	*L. tamdil* (Sengupta, Sailo, Lalremsanga, Das & Das, 2010)	Sengupta et al. 2010
84	*L. tengchongensis* (Yang, Wang, Chen & Rao, 2016)	Yang et al. 2016
85	*L. tuberosa* (Inger, Orlov & Darevsky, 1999)	Inger et al. 1999
86	*L. ventripunctata* (Fei, Ye & Li, 1990)	Fei et al. 1990; Fei et al. 2009, 2016
87	*L. wuhuangmontis* Wang, Yang & Wang, 2018	Wang et al. 2018
88	*L. wulingensis* Qian, Xia, Cao, Xiao & Yang, 2020	Qian et al. 2020
89	*L. yingjiangensis* (Yang, Zeng & Wang, 2018)	Yang et al. 2018
90	*L. yunkaiensis* Wang, Li, Lyu & Wang, 2018	Wang et al. 2018
91	*L. yeae* Shi, Hou, Song, Jiang & Wang, 2021	Shi et al. 2021
92	*L. yunyangensis* Luo, Deng & Zhou, 2022	Luo et al. 2022
93	*L. zhangyapingi* (Jiang, Yan, Suwannapoom, Chomdej & Che, 2013)	Jiang et al. 2013

Taxonomic account

Leptobrachella verrucosa Wang, Zeng, Lin & Li, sp. nov.

https://zoobank.org/D968B6DE-22B4-48D3-B3EC-DAFDB328BBD2

Figs 3, 4

Verrucous Leaf Litter Toad (in English) / Mi You Zhang Tu Chan (密疣掌突蟾 in Chinese)

Type material. ***Holotype*** ♂. GEP a062, collected by Shi-Shi Lin and Qi-Qi Zhang on 31 May 2022 from Lianshan Bijiashan Nature Reserve (24°12'49.63"N, 111°59'39.31"E; ca. 550 m a.s.l.), Lianshan County, Qingyuan City, Guangdong Province, China.

Paratypes. 4 ♂: GEP a059–061, 063, the same collection data as the holotype.

Etymology. The specific epithet "*verrucosa*" is an adjective meaning "verrucous", referring to the tuberculate dorsal skin texture of the new species.

Diagnosis. (1) Small body size [SVL 23.2–25.9 mm in five adult males], (2) iris bicolored, upper half coppery orange and lower half grayish brown, (3) tympanum distinct, (4) supratympanic line black, (5) fingers without lateral fringes, (6) toes with rudimentary webbing, lateral fringes narrow, (7) longitudinal ridges under toes continuous, (8) heels not meeting when adpressed, tibial-tarsal articulation reaching anterior corner of eye, (9) dorsal surface shagreened with numerous conical tubercles, lacking spines, enlarged warts or skin ridges, (10) ventral surface smooth, (11) dorsum grayish brown, with distinct darker brown scattered markings and irregular light orange pigmentations, (12) flanks with several dark spots, (13) ventral surface creamy white with grayish white and dark brown spots.

Description of holotype. Adult male. Body size small, SVL 23.2 mm. Head length slightly larger than head width, HDW/HDL 0.95; snout slightly protruding, projecting slightly beyond margin of lower jaw; nostril closer to snout than eye; canthus rostralis gently rounded; loreal region slightly concave; interorbital space flat, internarial distance slightly larger than interorbital distance, IND/IOD 1.05; pineal ocellus absent; pupil vertical; snout slightly longer than eye diameter, SNT/EYE 1.03; tympanum distinct, rounded, diameter smaller than that of eye and larger than tympanum-eye distance, TMP/EYE 0.54, TEY/TMP 0.46; upper margin of tympanum in contact with supratympanic ridge; vomerine teeth absent; a single vocal sac; vocal sac openings slit-like, paired, located posterolaterally on floor of mouth, close to margins of mandible; tongue deeply notched distally; supratympanic ridge distinct, extending from posterior corner of eye to supra-axillary gland.

Tips of fingers rounded, slightly swollen; relative finger lengths I = II = IV < III; nuptial pad absent;

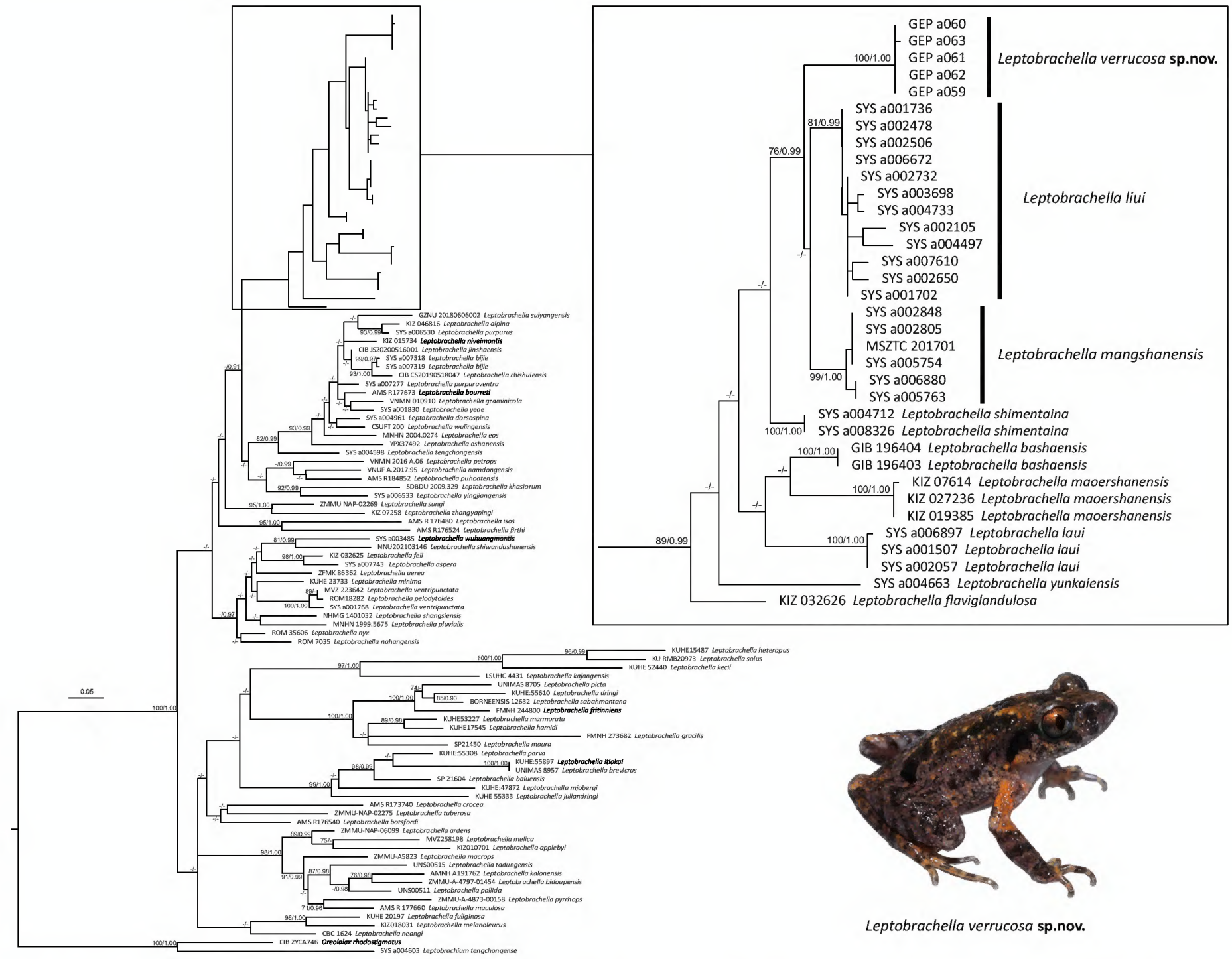

Figure 2. Bayesian inference Maximum Likelihood tree results from partial DNA sequences of the mitochondrial 16S r RNA gene. Numbers before slashes indicate bootstrap support (BS) and numbers after slashes are Bayesian posterior probabilities (BPP). The '-' represent BS ≤ 70 or BPP ≤ 0.90. Voucher before species name at the branch terminal corresponds to the voucher ID in Suppl. material 1: Table S1.

subarticular tubercles absent; inner palmar tubercle large, rounded, distinctly separated from outer palmar tubercle; outer palmar tubercle small, rounded; fingers lacking interdigital webbing and lateral fringes. Tips of toes rounded, slightly swollen; relative toe length I < II < V < III < IV; longitudinal ridges under toes continuous; inner metatarsal tubercle large, oval; outer metatarsal tubercle absent; interdigital webbing between toes rudimentary; narrow lateral fringes present on all toes. Tibia 49% of snout-vent length; tibiotarsal articulation reaches to anterior corner of eye; heels not meeting when thighs are appressed at right angles with respect to the body.

Dorsal surface shagreened with numerous conical tubercles, lacking spines, enlarged warts or skin ridges; ventral skin smooth; pectoral and femoral glands oval; both larger in diameter than tip of fingers; femoral glands larger in diameter than tip of toes; femoral gland situated on posteroventral surface of thigh, closer to knee than to vent; supra-axillary gland raised. Ventrolateral gland distinctly visible, forming a longitudinal uncontinuous series.

Coloration of holotype in life. Dorsal background color grayish brown, with distinct dark brown markings, and rounded spots, and scattered with irregular light orange pigmentation. A dark brown inverted triangular marking in interorbital region, connecting to dark brown W-shaped marking on occipital region. Tympanum dark brown, lower margin grayish white. Supratympanic line black. A pair of dark brown vertical bars present under eyes; transverse dark brown bars on dorsal surfaces of distal limbs and digits; distinct dark brown blotches on flanks; surfaces of elbows and upper arms coppery orange, with dark markings and spots.

Surface of throat, chest, belly and underside of forelimbs creamy white, with distinct grayish white and dark brown spots; under side of hindlimbs grayish purple with numerous white spots. Supra-axillary gland coppery orange, pectoral glands grayish white, femoral glands coppery orange, anterior half of ventrolateral glands coppery and posterior half grayish white. Iris bicolored, upper half coppery orange, lower half grayish brown.

Coloration of holotype in preservative. Dorsal background color dark brown scattered with irregular gray

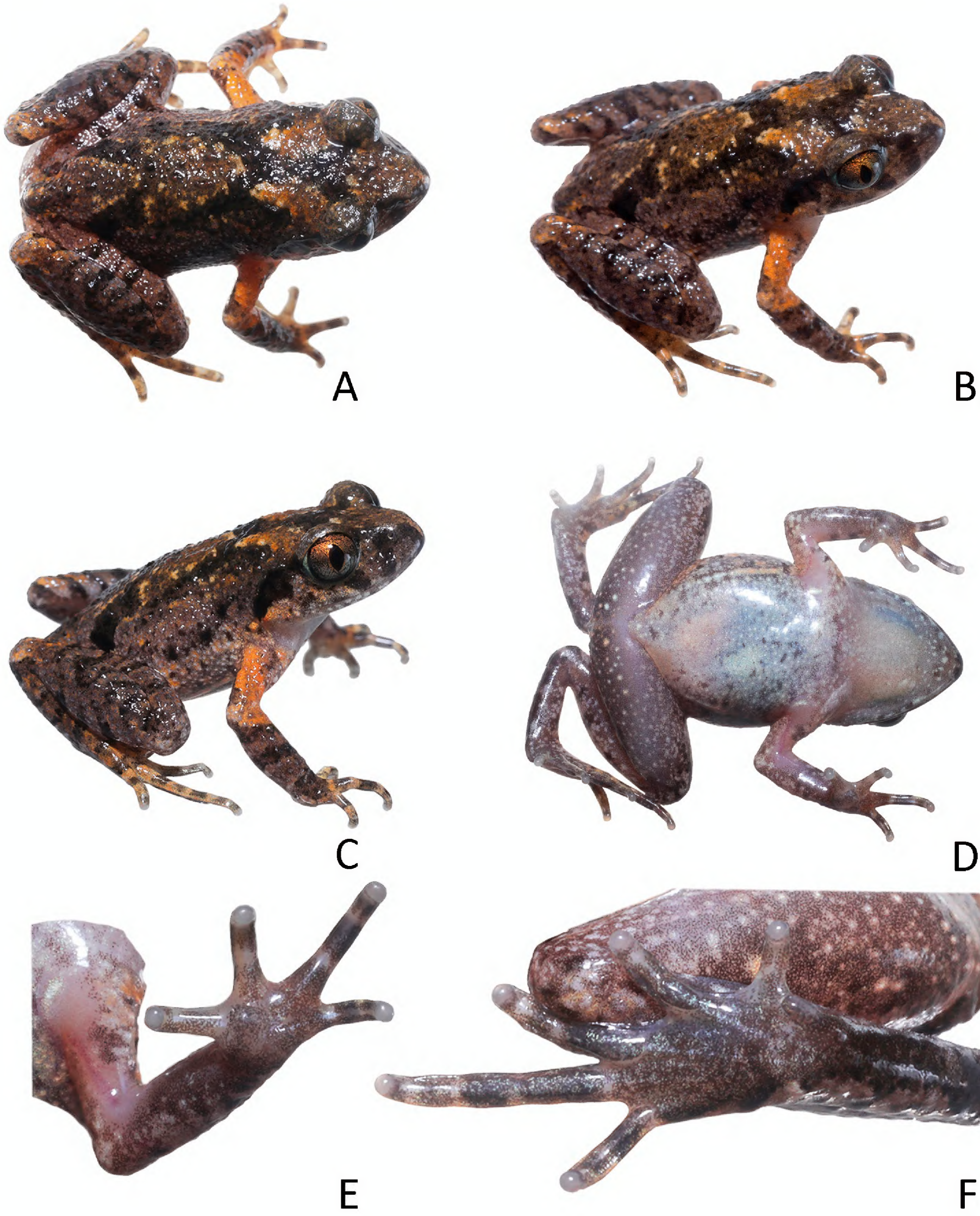

Figure 3. Morphological features of the holotype of *Leptobrachella verrucosa* sp. nov., GEP a062 in life: **A.** Dorsal view; **B.** Dorsolateral view; **C.** Lateral view; **D.** Ventral view; **E.** Ventral view of hand; **F.** Ventral view of foot.

pigmentations. All markings, bars and spots become indistinct. Tympanum dark brown.

Ventral surface grayish white; grayish white spots absent, dark brown spots become more distinct. Supra-axillary, pectoral, and ventrolateral glands greyish white.

Variation. Measurements and body proportions are listed in Table 2. The paratypes, GEP a059 (Fig. 4A), GEP a060 (Fig. 4B), and GEP a063 (Fig. 4D), show lighter coloration of markings and pigmentations on dorsum. The paratype, GEP a061 (Fig. 4C), possesses a more tuberculate dorsal skin texture. Pectoral glands much more distinct in all paratypes.

Distribution, ecology and conservation. *Leptobrachella verrucosa* sp. nov. is currently only

Table 2. Measurements (minimum-maximum (mean ± SD); in mm), and body proportions of *Leptobrachella verrucosa* sp. nov.

Vocher	GEP a059	GEP a060	GEP a061	GEP a062	GEP a063	Range
Sex	Male	Male	Male	Male	Male	Males (n = 5)
SVL	24.7	25.9	24.5	23.2	23.5	23.2–25.9 (24.4 ± 1.1)
HDL	9.5	10.1	9.8	9.2	9.3	9.2–10.1 (9.6 ± 0.4)
HDW	9.1	9.7	9.4	8.8	9.0	8.8–9.7 (9.2 ± 0.4)
SNT	4.0	4.1	3.9	3.1	3.2	3.1–4.1 (3.6 ± 0.5)
IND	2.7	2.8	2.7	2.5	2.6	2.5–2.8 (2.7 ± 0.1)
IOD	2.5	2.7	2.6	2.4	2.5	2.4–2.7 (2.5 ± 0.1)
EYE	3.6	3.7	3.5	3.0	3.1	3.0–3.7 (3.4 ± 0.3)
TMP	1.9	1.7	1.6	1.6	1.7	1.6–1.9 (1.7 ± 0.1)
TEY	0.9	1.0	0.8	0.8	0.8	0.8–1.0 (0.8 ± 0.1)
ML	6.8	6.8	6.7	6.3	6.2	6.2–6.8 (6.5 ± 0.3)
LAHL	12.7	12.8	12.7	11.9	12.0	11.9–12.8 (12.4 ± 0.4)
PL	11.2	11.7	11.5	10.7	10.8	10.7–11.7 (11.2 ± 0.4)
TIB	11.7	12.4	11.7	11.3	12.0	11.3–12.4 (11.8 ± 0.4)
HLL	38.6	40.0	36.7	36.6	38.1	36.6–40.0 (38.0 ± 1.4)

known from its type locality (Fig. 1; ca. 500–600 m a.s.l.) which is located at the boundary of Guangxi Zhuang Autonomous Region, and Guangdong and Hunan provinces. The new species inhabits clear-water rocky streams in primary forests surrounded by broad-leaved forest in granite landforms. Males were observed calling while perched on rocks or leaves of dwarf shrubs near flowing seeps. Data of larvae and females remain unknown. The breeding season lasts from April to June according to our long-term observation. We recommend the new species be listed as LC (Least Concerned) in the IUCN categorization as the forest is well protected and the distribution of the species is potentially wider than currently known, i.e. the adjacent Hunan Province and Guangxi Zhuang Autonomous Region.

Comparisons. In the phylogenetic tree (Fig. 2), *Leptobrachella verrucosa* sp. nov. is most closely related to the clade composed of *L. liui* and *L. mangshanensis*, therefore, the latter two are selected for detailed comparison (Table 3). The new species differs from *L. liui* by its narrow fringes along lateral surfaces of toes (vs. wide), continuous longitudinal ridges under toes (vs. interrupted), dorsal surface with numerous conical tubercles and lacking skin ridges (vs. dorsal surface with rounded warts and sparse short skin ridges), heels not meeting when adpressed (vs. heels meeting). The new species differs from *L. mangshanensis* by its shagreened dorsal surface with numerous conical tubercles, lacking spines, enlarged warts or skin ridges (vs. dorsal surface almost smooth with tiny transparent spines, small tubercles and sparse short skin ridges), ventral surface of thighs lacking conical spines (vs. ventral surface bearing conical spines), tibial-tarsal articulation reaching anterior corner of eye (vs. reaching tip of snout, well beyond anterior corner of eye).

Leptobrachella verrucosa sp. nov. can be distinguished from *L. yunkaiensis* and *L. shimentaina* by having no fringes along lateral surfaces of fingers (vs. lateral fringes present in *L. yunkaiensis* and males of *L. shimentaina*); narrow fringes along lateral surfaces of toes (vs. lateral fringes wide in *L. yunkaiensis* and males of *L. shimentaina*); shagreened dorsal surface with numerous conical tubercles, lacking spines, enlarged warts or skin ridges (vs. dorsal surface with skin ridges in *L. shimentaina*, dorsal surface with short skin ridges and raised warts in *L. yunkaiensis*); heels not meeting when adpressed (vs. heels slightly overlapping in *L. shimentaina*, heels meeting in *L. yunkaiensis*). *Leptobrachella verrucosa* sp. nov. can be distinguished from *L. bashaensis* and *L. maoershanensis* by having shagreened dorsal surface with numerous conical tubercles, lacking spines, enlarged warts or skin ridges (vs. dorsum shagreened with small tubercles in *L. bashaensis*, dorsum with skin ridges in *L. maoershanensis*); tibial-tarsal articulation reaching anterior corner of eye (vs. reaching tip of snout, well beyond anterior corner of eye in *L. bashaensis* and *L. maoershanensis*). *Leptobrachella verrucosa* sp. nov. can be distinguished from *L. laui* by having no lateral fringes along lateral surfaces of fingers (vs. moderate lateral fringes present), narrow lateral fringes along lateral surfaces of toes (vs. lateral fringes wide). *Leptobrachella verrucosa* sp. nov. differs from *L. flaviglandulosa* by having continuous longitudinal ridges under toes (vs. interrupted), heels not meeting when adpressed (vs. heels meeting).

Compared with the 26 known congeners of the genus *Leptobrachella* occurring south of the Isthmus of Kra, by the presence of supra-axillary and ventrolateral glands, *L. verrucosa* sp. nov. can easily be distinguished from *L. arayai*, *L. dringi*, *L. fritinniens*, *L. gracilis*, *L. hamidi*, *L. heteropus*, *L. kajangensis*, *L. kecil*, *L. marmorata*, *L. melanoleuca*, *L. maura*, *L. picta*, *L. platycephala*, *L. sabahmontana*, and *L. sola*, all of which lack supra-axillary and ventrolateral glands; and by its distinctly larger male body size, SVL 23.2–25.9 mm, *L. verrucosa* sp. nov. differs from the smaller *L. baluensis* (SVL 14.9–15.9 mm), *L. brevicrus* (SVL 17.1–17.8 mm), *L. bondangensis* (SVL 17.8 mm), *L. fusca* (SVL 16.3 mm), *L. itiokai* (SVL 15.2–16.7 mm), *L. juliandringi* (SVL 17.0–17.2 mm), *L. mjobergi* (SVL 15.7–19.0 mm), *L. natunae* (SVL 17.6 m), *L. parva* (SVL 15.0–16.9 mm), and *L. palmata* (SVL 14.4–16.8 mm); and even distinctly larger than female *L. serasanae* (SVL 16.9 mm).

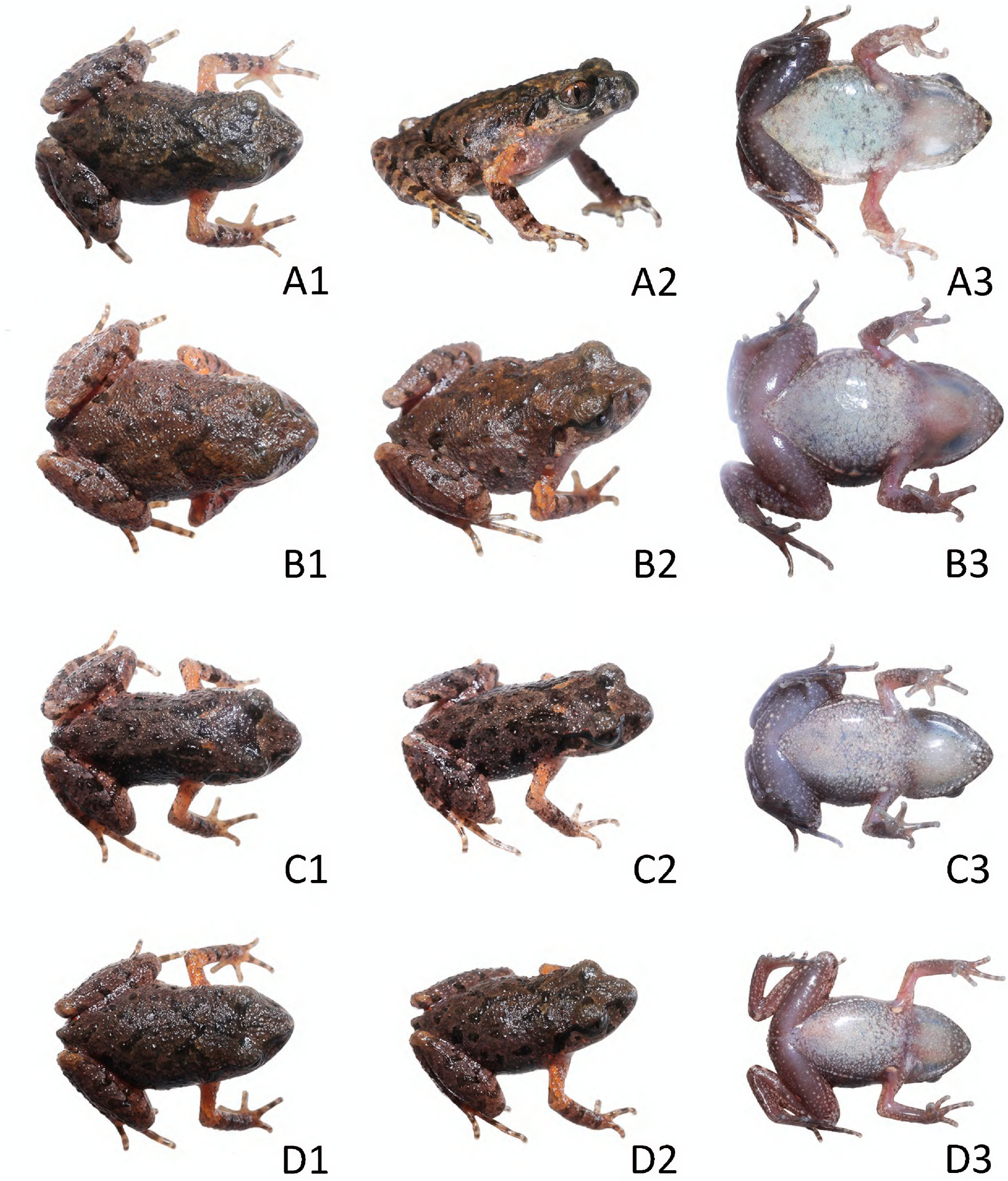

Figure 4. Morphological features of the paratypes of *Leptobrachella verrucosa* sp. nov., in life: **A.** GEP a059 (**A1** dorsal view, **A2** lateral view, **A3** ventral view); **B.** GEP a060 (**B1** dorsal view, **B2** dorsolateral view, **B3** ventral view); **C.** GEP a061 (**C1** dorsal view, **C2** dorsolateral view, **C3** ventral view); **D.** GEP a063 (**D1** dorsal view, **D2** dorsolateral view, **D3** ventral view).

In having black spots on flanks, *Leptobrachella verrucosa* sp. nov. further differs from *L. aerea*, *L. botsfordi*, *L. crocea*, *L. firthi*, *L. isos*, *L. pallida*, *L. petrops*, and *L. tuberosa*, all of which lack black spots on the flanks.

For the remaining 54 members of the genus *Leptobrachella*, males of the new species (SVL 23.2–25.9 mm) differs from males of the larger *L. bijie* (29.0–30.4 mm), *L. chishuiensis* (30.8–33.4 mm), *L. bourreti* (27.4–36.2 mm), *L. damingshanensis* (33.6–34.4 mm), *L. dorsospina* (28.7–30.5 mm), *L. eos* (33.1–34.7 mm), *L. fuliginosa* (28.2–30.0 mm), *L. jinshaensis* (29.7–31.2 mm), *L. macrops* (28.0–29.3 mm), *L. nahangensis* (40.8 mm), *L. namdongensis* (30.9 mm), *L. pelodytoides* (27.5–32.3 mm), *L. purpuraventra* (27.3–29.8 mm),

Table 3. Comparisons of selected diagnostic characters for the new species and its phylogenetically related congeners.

Leptobrachella spp.	Fringes on fingers (present + / absent -)	Fringes on toes	Longitudinal ridges under toes (interrupt + / continuous -)	Ventral coloration	Dorsal skin texture
L. verrucosa sp. nov.	-	Narrow	-	Creamy white with grayish white and dark brown spots	Shagreened with numerous conical tubercles
L. bashaensis	-	Narrow	-	Creamy-white chest and belly with irregular black spots	Slightly shagreened with small tubercles
L. flaviglandulosa	-	Narrow	+	Whitish, black speckling on margins	Shagreened with yellowish-brown tubercles
L. laui	+	Wide	-	Creamy white with dark brown dusting on ventrolateral flanks	Shagreened with round granular tubercles
L. liui	-	Wide	+	Gray white to creamy white with dark brown spots on chest and ventrolateral flanks	Shagreened with numerous small tubercles, round warts and sparse short skin ridges
L. mangshanensis	-	Narrow	-	Creamy white belly, scattered with white speckles	Almost smooth with tiny transparent spines, small tubercles and sparse short skin ridges
L. maoershanensis	-	Narrow	-	Creamy white chest and belly with irregular black spots	With longitudinal ridges
L. shimentaina	+ (in males)	Wide (in males)	-	Grayish pink with distinct hazy brown speckling on chest and ventrolateral flanks	Shagreened with rounded granular tubercles and glandular ridges
L. yunkaiensis	+	Wide	-	Belly pink with distinct or indistinct speckles	Shagreened with short skin ridges and raised warts

L. pyrrhops (30.3–33.9 mm), *L. suiyangensis* (28.7–29.7 mm), *L. sungi* (48.3–52.7 mm), *L. yunyangensis* (28.3–30.6 mm), and *L. zhangyapingi* (48.5–52.5 mm). Through its possession of toes with rudimentary webbing and narrow lateral fringes, the new species can be distinguished from *L. ardens*, *L. kalonensis*, *L. maculosa*, *L. neangi*, *L. rowleyae*, *L. shiwandashanensis*, and *L. tadungensis* (no webbing); male *L. alpina*, *L. graminicola*, *L. khasiorum*, *L. murphyi*, *L. purpurus*, and *L. yingjiangensis* (wide lateral fringes); *L. applebyi*, *L. lateralis*, *L. melica*, *L. minima*, *L. nyx*, *L. oshanensis*, *L. pluvialis*, and *L. ventripunctata* (no lateral fringes). In having shagreened dorsal surface with numerous conical tubercles, lacking spines, enlarged warts or skin ridges, it can be distinguished from *L. aspera*, *L. feii*, *L. nokrekensis*, *L. puhoatensis*, *L. tengchongensis*, *L. wuhuangmontis*, and *L. wulingensis* (dorsum with skin ridges). In having creamy white ventral surface with grayish white and dark brown spots, it can be distinguished from *L. bidoupensis* (ventral surface reddish brown), *L. niveimontis* (ventral surface marbling), *L. shangsiensis* (ventral surface yellowish creamy-white with marble patterns), and *L. tamdil* (abdominal region unpatterned). In having continuous longitudinal ridges under toes, it can be distinguished from *L. yeae* (longitudinal ridges under toes interrupted).

Discussion

Leptobrachella pelodytoides (Boulenger, 1893) was described from Thao [= Thamo], Kayah State, Myanmar. Pope (1931) first reported *L. pelodytoides* in China based on a series of specimens from Fujian Province. The identification was revised by Fei and Ye (1992) and it was recognized as a distinct species, *L. liui*. Fei et al. (2009) further extended the known distribution of *L. liui* to Guangxi Zhuang Autonomous Region, Fujian, Zhejiang, Jiangxi, Hunan, and Guizhou Provinces, and two localities bordering Guangdong, i.e. Hunan Province (Yizhang county) and Hong Kong. Later, Li et al. (2011) recognized *Leptobrachella* populations from Hong Kong and Guangdong Province (Xinyi City, Fengkai County, Shenzhen City) as *L. pelodytoides* (Boulenger, 1893). However, all these proposals, excluding the record from Fengkai County, have since been revised: (1) the *Leptobrachella* population from Hong Kong and adjacent Shenzhen City of Guangdong Province should actually be *L. laui* (Sung et al. 2014), neither *L. pelodytoides* nor *L. liui*; (2) the population recorded as *L. liui* from Hunan Province was revised as *L. mangshanensis* (Hou et al. 2018), which was confirmed to occur in northern Guangdong Province by Wang et al. (2022); (3) the population recorded as *L. pelodytoides* from Xinyi City was revised as *L. yunkaiensis* by Wang et al. (2018); (4) Wang et al. (2022) further described a new species from northern Guangdong Province, *L. shimentaina*, which was indicated by Chen et al. (2018) as a putatively undescribed species "*Leptobrachella* sp. 6" (refer to Suppl. material 1: Table S1 and Fig. 1 for detailed distribution information). The taxonomic status of the population from Fengkai County, western Guangdong remains unresolved due to the lack of morphological and molecular data and the distribution of *L. pelodytoides* in China has been indirectly ruled out (Ohler, 2011; Chen et al. 2017). Thus, we propose to remove *L. pelodytoides* from the herpetofauna of Guangdong Province. Most importantly, the historic records of *L. liui* and *L. pelodytoides* from other areas require reevaluation.

Below, we provide a key for all species within the genus *Leptobrachella* occurring in Guangdong Province, which includes *L. laui*, *L. liui*, *L. mangshanensis*, *L. shimentaina*, *L. yunkaiensis*, and *L. verrucosa*.

Key to *Leptobrachella* species occurring in Guangdong Province, China

1 Longitudinal ridges under toes interrupted ..... *L. liui*
– Longitudinal ridges under toes continuous 2
2 Fingers without lateral fringes, toes with narrow lateral fringes in males 3
– Fingers with lateral fringes, toes with wide lateral fringes in males 4
3 Dorsal skin almost smooth with tiny transparent spines, small tubercles and sparse short skin ridges .....*L. mangshanensis*
– Dorsal skin shagreened with numerous conical tubercles, lacking spines, enlarged warts or skin ridges ..... *L. verrucosa*
4 Dorsal skin lacking skin ridges, ventral coloration white ..... *L. laui*
– Dorsal skin with skin ridges, ventral coloration pink 5
5 Dorsal skin shagreened with rounded granular tubercles, longitudinal ridges under toes with constrictions at interphalangeal articulations ..... *L. shimentaina*
– Dorsal skin shagreened with raised and enlarged warts, longitudinal ridges under toes without constrictions at interphalangeal articulations ..... *L. yunkaiensis*

Acknowledgements

We thank Günter Gollmann and two anonymous reviewers for their constructive comments on the manuscript. This work was supported by the Project of Background survey of biosafety in Guangdong Province (STST-2021-10), the Project of Study on optimal allocation and sustainable development of typical urban and rural ecological resources (K610222062406), and the Project of Diversity monitoring on flora and fauna in Guangdong Lianshan Bijiashan Provincial Nature Reserve.

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Appendix 1

Specimens examined

Leptobrachella laui **(n = 26):** China: Hong Kong: SYS a002057 (Holotype), SYS a002058; China: Guangdong: Shenzhen City: SYSa 001505–1507, 1515–1521, 3471–3472, 5644–5645.

Leptobrachella liui **(n = 32):** China: Fujian: Mt. Wuyi: SYS a001572, 1596, 2478, 2479, 5925, 5926; China: Fujian: Mt. Daiyun: SYS a001736, 6010; China: Fujian: Mt. Longqi: SYS a002505, 2506; China: Guangdong: Mt. Tongguzhang: SYS a004733–4735; China: Guangdong: Mt. Fenghuang: SYS a003698–3699; China: Guangdong: Mt. Motianshi: SYS a007610–7613; China: Guangdong: Mt. Nankun: SYS a002020, 4497; China: Guangdong: Gutian Nature Reserve: SYS a002650; China: Jiangxi: Mt. Jiulian: SYS a002104–2105; China: Jiangxi: Mt. Tongbo: SYS a001702, 2059; China: Jiangxi: Mt. Yangjifeng: SYS a006667, 6672; China: Zhejiang: Jingning: SYS a002732–2735.

Leptobrachella mangshanensis **(n = 11):** China: Hunan: Mangshan Nature Reserve: SYS a008366; China: Guangdong: Nanling Nature Reserve: SYS a002828–2830, 5754; China: Guangdong: Shimentai Nature Reserve: SYS a005763, 6880; China: Guangdong: Mt. Tianjing: SYS a002806, 2809; China: Guangdong: Mt. Dadong: SYS a002847–2848.

Leptobrachella yunkaiensis **(n = 8):** China: Guangdong: Maoming City: Mt. Yunkai: SYS a004664/CIB107272, SYS a004663, 4665–4669, 4690.

Supplementary material 1

Table S1

Authors: Shi-Shi Lin, Yuan-Hang Li, Yu-Hong Lu, Hong-Lin Su, Shi-Bin Wu, Qi-Qi Zhang, Mei-Juan Mo, Shao-Jun Xiao, Zhong Pan, Hu-Jun Pan, Zhao-Chi Zeng, Jian Wang

Data type: Excel files

Explanation note: Collection localities, voucher data, and Genbank numbers (16S rRNA) for all *Leptobrachella* samples used in this study.

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Link: https://doi.org/10.3897/herpetozoa.35.e89981.suppl1

Supplementary material 2

Table S2

Authors: Shi-Shi Lin, Yuan-Hang Li, Yu-Hong Lu, Hong-Lin Su, Shi-Bin Wu, Qi-Qi Zhang, Mei-Juan Mo, Shao-Jun Xiao, Zhong Pan, Hu-Jun Pan, Zhao-Chi Zeng, Jian Wang

Data type: Excel files

Explanation note: Pairwise mean distances based on 16S gene among all sample used in this study.

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